Biological motion drives perception and action

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Presenting a few dots moving coherently on a screen can yield to the perception of human motion. This perception is based on a specific network that is segregated from the traditional motion perception network and that includes the superior temporal sulcus (STS). In this study, we investigate whether this biological motion perception network could influence the smooth pursuit response evoked by a point-light walker. We found that smooth eye velocity during pursuit initiation was larger in response to the point-light walker than in response to one of its scrambled versions, to an inverted walker or to a single dot stimulus. In addition, we assessed the proximity to the point-light walker (i.e. the amount of information about the direction contained in the scrambled stimulus and extracted from local motion cue of biological motion) of each of our scrambled stimuli in a motion direction discrimination task with manual responses and found that the smooth pursuit response evoked by those stimuli moving across the screen was modulated by their proximity to the walker. Therefore, we conclude that biological motion facilitates smooth pursuit eye movements, hence influences both perception and action.

Keywords: smooth pursuit, biological motion, motion perception, point-light animation, action perception, pursuit initiation

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Introduction

Humans are able to perceive human motion and infer a person's intentions from it (Blake & Shiffrar, 2007). This ability is often studied by showing human subjects a movie of the movement of dots attached to the body joints of a human actor or an animal performing a particular action, referred to as biological motion (e.g., walking, Johansson, 1973). Due to its particular importance, biological motion is probably processed differently by the visual system than other kinds of motion stimuli (Billino, Braun, Böhm, Bremmer, & Gegenfurtner, 2009; Decety & Grezes, 1999; Giese & Poggio, 2003; Oram & Perrett, 1994). Indeed, several electrophysiological (Jellema, Maassen, & Perrett, 2004; Perrett et al., 1985) and imaging studies (Grezes et al., 2001; Grossman, Battelli, & Pascual-Leone, 2005; Grossman & Blake, 2001, 2002; Grossman et al., 2000; Pelphrey et al., 2003; Saygin, 2007; Saygin, Wilson, Hagler, Bates, & Sereno, 2004) support the hypothesis of one or several specific neural pathways for biological motion perception. Indeed, biological motion perception is subserved by a bottom-up and a top-down mechanism (Blake & Shiffrar, 2007; Troje, 2008). The bottom-up mechanism processes local motion cues and probably originates in early areas of the visual pathway (Johansson, 1973; Troje & Westhoff, 2006). In contrast, the top-down mechanism is based on configural processing, hence on structure-from-motion mechanisms (Beintema & Lappe, 2002; Bertenthal & Pinto, 1994; Thornton, 1998).

In several instances, perception and smooth pursuit eye movements have been shown to share motion integration mechanisms (Krauzlis & Stone, 1999). For example, perception of motion direction and steady-state pursuit eye movements (>300 ms after stimulus onset) exhibited similar directional thresholds (Beutter & Stone, 1998; Stone, Beutter, & Lorenceau, 2000; Stone & Krauzlis, 2003). In the same vein, pursuit and perception variability are similar during steady-state pursuit (Rasche & Gegenfurtner, 2009). During the open-loop phase of the pursuit response (<300 ms with respect to stimulus onset), pursuit exhibits a directional bias that is similar to perception (Masson, 2004; Masson & Stone, 2002), but with much less sensitivity to speed (Rasche & Gegenfurtner, 2009). In

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sum, the link between pursuit and perception evolves over time. During initiation, pursuit is very sensitive to low-level motion cues whereas it becomes more sensitive to higher-level motion later, i.e. after the first catch-up saccade (Wilmer & Nakayama, 2007). Speed and direction of motion are essentially processed in the middle temporal area (MT; Born & Bradley, 2005), which is one of the main inputs to the smooth pursuit system (Ilg & Thier, 2008; Lencer & Trillenberg, 2008; Orban de Xivry & Lefèvre, 2007).

The above-mentioned studies focused on the link between motion perception and smooth pursuit. In this study, we investigated whether biological motion perception that is not processed by the conventional motion processing network (Mcleod, Dittrich, Driver, Perrett, & Zihl, 1996; Vaina, Lemay, Bienfang, Choi, & Nakayama, 1990), influenced smooth pursuit eye movements. To do so, we proceeded in three different steps. First, we compared smooth pursuit eye movements elicited by a point-light walker and by some control stimuli. We hypothesized that the biological motion stimulus might either decrease smooth pursuit latency or increase eye velocity. Both scrambled or inverted point-light walkers were used as control stimuli as they disrupt different aspects of biological motion perception (i.e., local motion is preserved in the scrambled stimuli but not in inverted walkers whereas inversion preserves configural features such as opponent movements of the feet) and their vision activates differentially the STS region (Grossman & Blake, 2001). Second, we assessed the sensitivity of the smooth pursuit system to the proximity of the stimuli to the walker. In this respect, we correlated results from the behavioral experiment and from a psychophysics experiment. In the latter, the proximity to the walker was defined as the amount of information about the direction contained in the scrambled stimulus and extracted from local motion cue of biological motion. This proximity was assessed by determining how accurately subjects could indicate the walking direction of the different scrambled walkers. The strong correlation between the output measures of the behavioral and psychophysics experiments suggests that attentional factors cannot explain the difference in behaviors elicited by the different stimuli. Finally, given that smooth pursuit eye movements were faster for the biological motion stimuli, compared to the control stimuli, we investigated whether the point-light walker facilitated or the control stimuli deteriorated smooth pursuit eye movements. In this respect, we compared smooth pursuit eye movements elicited either by those stimuli or by a single dot moving at a comparable speed. We found that biological motion perception facilitated smooth pursuit eye movements. Therefore, we concluded that, similarly to motion perception, biological motion perception influences smooth pursuit eye movements. This suggests that the biological motion network functions as an input to the smooth pursuit system and demonstrates that biological motion can affect both perception and action.

Materials and methods

Thirteen human subjects (9 males) participated in the experiments after informed consent. They were between 20 and 42 years old. Six of them had never participated in oculomotor experiments. All procedures were approved by the Université catholique de Louvain Ethics Committee and were in agreement with the Declaration of Helsinki.

Stimuli

Our experiments involved a biological motion stimulus (point-light walker) and some control stimuli. Movies of those stimuli are available in the supplementary material. The motion of the 11 dots of the point-light walker was computed using Cutting's algorithm (Figure 1) (Cutting, 1978). Therefore, the trajectory of each point can be described as a pair of functions:

$$\left(x_i^{BM}(t),\ y_i^{BM}(t)\right) where\ y_i^{BM}(t) = y_i^{local}(t) + \bar{y}_i. \quad (1)$$

Here, y_i^{local} represents the local vertical motion of the point around its mean vertical position ($\bar{y}_i$). The scrambled walker was obtained by shuffling the mean vertical position ($\bar{y}_i$) of the dots (except the hip dot) to disrupt the global form, while keeping the same local motion (y_i^{local}). Therefore, the trajectories of the dots for the scrambled walker were defined as follows:

$$\begin{aligned} & x_i^{SCR}(t) = x_i^{BM}(t)\ for\ all\ i \\ \left(x_i^{SCR}(t), y_i^{SCR}(t)\right)\ where\ & y_i^{SCR}(t) = y_i^{BM}(t)\ if\ i = hip \\ & y_i^{SCR}(t) = y_i^{local}(t) + \bar{y}_k\ if\ i \neq hip\,. \end{aligned} \quad (2)$$

The association between 'k' and 'i' was determined by random permutation of 'i' and differed for each scrambled stimulus. The inverted stimulus was obtained by flipping the original point-light walker upside-down:

$$\begin{aligned} x_i^{INV}(t) &= x_i^{BM}(t)\ for\ all\ i \\ y_i^{INV}(t) &= -y_i^{BM}(t)\ for\ all\ i\,. \end{aligned} \quad (3)$$

Whatever the stimulus type, the hip dot (highlighted in green) followed an identical trajectory and subjects were asked to track this particular dot. The different stimulus

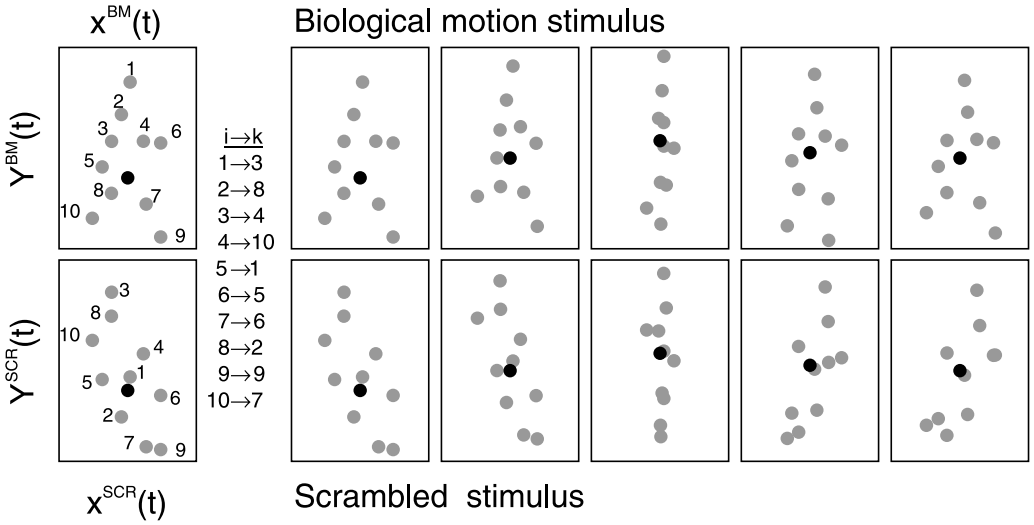


Figure 1. Representative pictures of the biological and scrambled walkers used in this study. On the left, we describe the algorithm used to produce scrambled stimuli and provide the correspondence table between the two stimuli as explained in Materials and methods. On the right, the upper panels represent five pictures of the biological motion stimulus, whereas the lower panels depict five pictures of an example of a scrambled stimulus (picture interval: 150 ms). The hip point that the subjects were asked to pursue is represented in black.

speeds were obtained by varying the step size of the walker.

Procedure

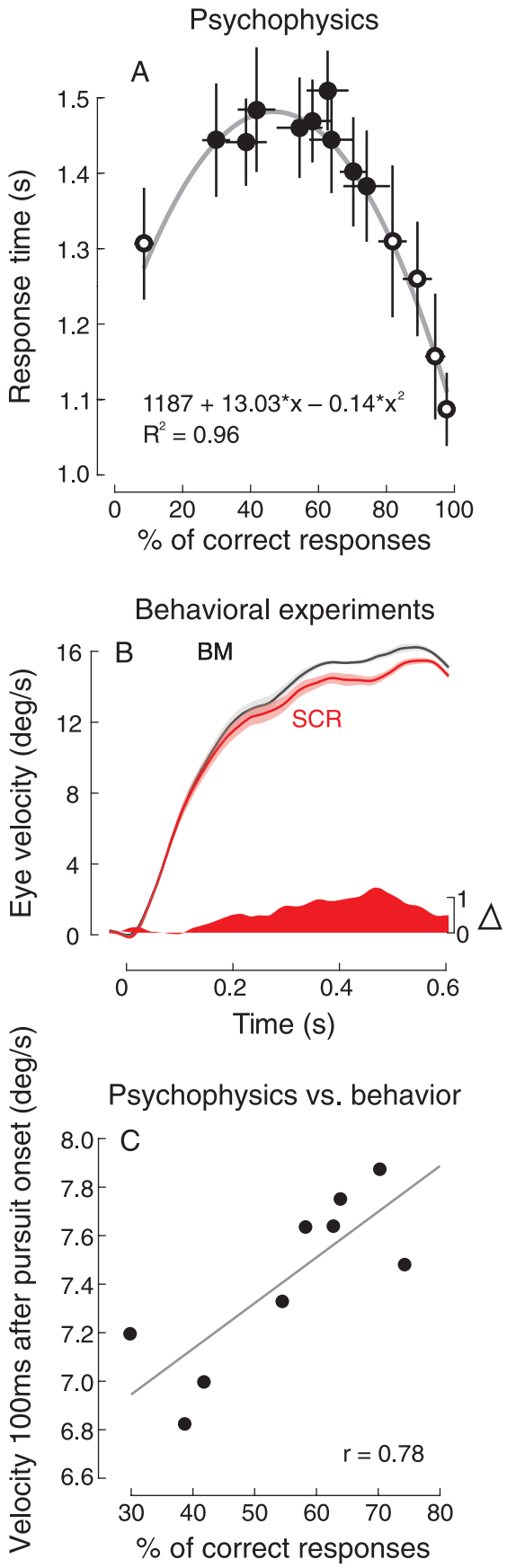
We conducted one psychophysics and two behavioral experiments. In the psychophysics experiment, ten subjects were required to indicate the heading direction (i.e. the direction of walking) of an animated, but stationary (as if on a treadmill), point-light stimulus presented on the screen (7.2° in height). For each trial, the stimulus was chosen randomly among a set of 14 scrambled stimuli plus the point-light walker, and the heading direction of the associated walker was randomized. Because each scrambled stimulus was obtained from a biological motion stimulus (see above), we considered the heading direction of the scrambled stimulus as the heading direction of its original point-light walker stimulus. The animation of the dots around the hip dot was similar to when the walker was moving at a speed of 10°/s (see behavioral experiments below) but the hip dot remained stationary.

In the first behavioral experiment, after a period of fixation, eight subjects from the psychophysics experiment were asked to pursue the hip dot of either a moving point-light walker or one of its scrambled versions. The stimulus moved either to the left or to the right at a velocity of 5, 10 or 15°/s for 800 ms (measured as the average velocity of the hip dot, see below). The type of stimulus, its direction, and its velocity were selected at random for each trial. The facing direction of the stimulus was always congruent with its direction of motion. For each block, the scrambled walker stimulus was chosen randomly from a set of possible stimuli consisting of nine stimuli selected from the psychophysics experiment (see Results).

The second behavioral experiment was very similar to the first, except that the scrambled control stimuli were replaced by an upside-down point-light walker. Ten subjects participated in this experiment, five of whom had already performed the first experiment. During the same session, 7 out of the ten subjects performed a few more trials during which the hip dot only was presented (DOT stimulus). For those trials, the motion of the hip dot corresponded to a stimulus moving at 15°/s. On average, we obtained 360 valid trials per subject for the point-light walker stimulus, 300 for the scrambled stimuli, 65 for the inverted stimulus and 63 for the DOT stimulus.

Data collection and analysis

Subjects sat in a dark room in front of a large screen that spanned 50° of their visual field and was 1.5 m away. Their head was restrained by a chin-rest. Stimuli were projected onto the screen with a cine8 Barco projector (Refresh rate: 100 Hz; Barco NV, Belgium) that was controlled by a VSG graphic card, in real time (Cambridge Research System Ltd, UK). Eye movements were recorded at 200 Hz using a Chronos Eye Tracker (Skalar Medical BV, The Netherlands) and with an Eyelink 1000 (SR Research Ltd., Ottawa, Ontario, Canada) at 1000 Hz for three subjects. Eye movements were low-pass filtered at 45 Hz using a zero-phase digital filter (auto-regressive forward-backward filter), and velocity and acceleration signals were derived from position signals using a central difference algorithm with a ±10 ms interval. Saccades,



which were detected using a 500°/s^2 threshold on the vectorial acceleration, were removed from the smooth eye velocity trace (see details in de Brouwer, Missal, Barnes, & Lefèvre, 2002). Since the vertical component of eye velocity remained below 3 deg/s, the rest of the analyses focused on the horizontal component of eye velocity or saccade amplitudes. Pursuit onset was determined by fitting a piece-wise linear function on the eye velocity trace measured during an interval of 250 ms starting at stimulus onset:

$$f(t) = \begin{cases} A & if\ t < T \\ B \cdot (t - T) & if\ t \geq T \end{cases}, \quad (4)$$

where t was the time (s), T is the time of pursuit onset (s), A the level of eye velocity before pursuit onset (°/s) and B the mean acceleration during pursuit initiation (°/s^2). The constants A, B and T were the free parameters of the function. The average values of A and B were 0.03°/s and 65°/s^2. Trials were visually inspected, and trials with blink, saccades before pursuit onset, etc. were discarded.

In the psychophysics experiment, we analyzed the response time and the percentage of correct answer. In the behavioral experiments, we analyzed smooth eye velocity, pursuit latency and catch-up saccade latency, accuracy (horizontal position error at the end of the saccade) and amplitude. For the purposes of statistical analyses, we calculated intra-subject means for selected measures. Similarly, the average profiles shown on Figures 2B and 3 were obtained by averaging, across subjects, their intra-subject means for the highest stimulus velocity. We used repeated measures ANOVA on the intra-subjects means of those measures with stimulus type

Figure 2. A) Relationship between the average response time and the average percentage of correct responses across subjects measured during the psychophysics experiment. Each dot represents a different scrambled point-light walker. The line represents a parabola that was fit to the data, for which the equation was inserted in the panel. The filled dots were those considered for the subsequent analyses (panels B and C). Error bars represent standard error of the mean. B) Average smooth eye velocity profiles (thin lines) evoked either by the biological motion stimuli (BM, black) or by the control stimuli (SCR, scrambled point-light walker, in red) for all subjects pooled together. Areas surrounding the traces represent confidence intervals. In the inset, we describe the difference between the two average profiles presented in the corresponding panel. Trials were aligned at smooth pursuit onset (time 0), prior to averaging. Stimulus velocity was 15°/s. C) Correlation between the percentage of correct responses reported during the psychophysics experiment and the smooth eye velocity measured 100 ms after pursuit onset during the behavioral experiment. Each dot represents one scrambled stimulus and represents the average across subjects. Stimulus velocity was 15°/s.

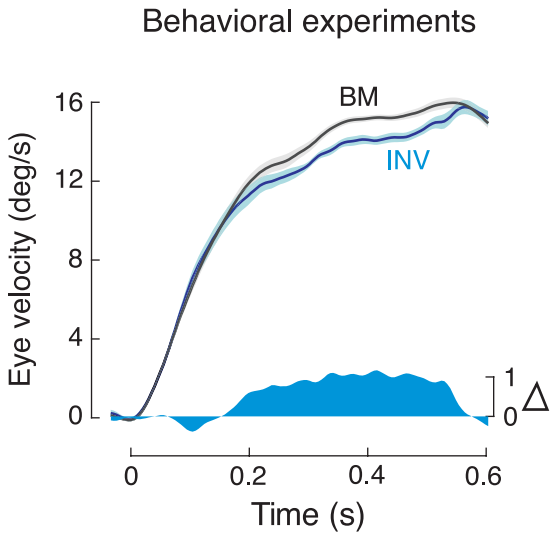


Figure 3. Average smooth eye velocity profiles (thin lines) evoked either by the biological motion stimuli (BM, black) or by the control stimuli (INV, inverted point-light walker in blue) for all subjects pooled together. Areas surrounding the traces represent confidence intervals. In the inset, we describe the average difference between the two curves presented in the corresponding upper panels (average BM profile minus average INV profile). Trials were aligned at smooth pursuit onset (time 0), prior to averaging. Stimulus velocity was 15°/s.

and velocity as within-subject factors. Tukey's Post Hoc test was used to evaluate one-to-one differences. Statistical analyses were performed with Statistica (Statsoft, Tulsa, OK).

Results

Scrambling disrupts biological motion perception

Scrambling the dots of the point-light walker impaired the biological relevance of the stimulus, but this impairment might depend on the scrambling method. Therefore, we investigated the proximity to the walker stimulus of our 14 scrambled stimuli in a motion direction discrimination task; subjects had to indicate the heading direction of the displayed stimulus by pressing a button that recorded both their responses and their response times. We found a strong relationship between those two measures (Figure 2A). The parabola (R^2 = 0.96) that fit those points indicated that the maximum response time was close to the maximum uncertainty about motion direction (maximum of uncertainty: 50% correct responses; maximum of the parabola at x = 46.3). In some instances, the more stimulus direction was ambiguous, the more uncertain subjects were about the specific direction and the more time it took them to indicate the direction in which the stimulus was heading. On the other hand, some stimuli were less ambiguous and the response time was shorter. In these cases, uncertainty was reduced, even if the directions reported were wrong (uttermost left point on Figure 2A). Nonetheless, the uncertainty about stimulus direction was much larger for any scrambled stimulus than for the point-light walker, as indicated by the longer reaction time for scrambled stimuli (>1088 ms), compared to the response time for the biological motion stimulus (inter-subject mean: 754 ms, inter-subject standard deviation *SD*: 106 ms). To avoid confounding results that may arise from differences in uncertainty about motion direction in our behavioral experiment, we focused on the nine stimuli with the maximum uncertainty (25–75% of correct answers).

The smooth pursuit response is influenced by the stimulus type

To test whether proximity to the walker affected the reactive smooth pursuit response in human subjects, we recorded the smooth pursuit response elicited by a biological point-light walker (BM) or by a control stimulus that was a scrambled version of the point-light walker (SCR; nine possible stimuli; black dots in Figure 2A). We predicted that the biological motion content of the stimulus might influence the latency of the motor response and/or its strength. We found that the latency of the smooth pursuit response was not influenced by the stimulus type (BM: 113 ms; SCR: 116 ms; ANOVA: $F(1, 7) = 3.57$, $p = 0.1$). In contrast, the stimulus type strongly influenced the velocity of smooth pursuit eye movements, as can be seen in Figure 2B (and Figure S1), which shows the inter-subject average of eye velocity as a function of time for the BM and SCR stimuli (time was synchronized with pursuit onset). A repeated measures ANOVA, with stimulus type (BM or SCR) and velocity as within-subject factors, indicated that, 150 ms after pursuit onset, there was a significant main effect of stimulus type on smooth eye velocity ($F(1, 7) = 14.78$, $p = 0.006$), whereas the interaction between stimulus type and speed was not ($F(2, 14) = 0.81$, $p = 0.46$). Therefore, 150 ms after pursuit onset, smooth eye velocity evoked by biological motion was significantly higher than smooth eye velocity evoked by the scrambled stimuli for all stimulus velocities. Fifty milliseconds earlier, there was already a trend for the influence of stimulus type on smooth eye velocity as early as 100 ms after pursuit onset (ANOVA: $F(1, 7) = 4.91$, $p = 0.06$). As shown in Figure 2B, the facilitating effect of biological motion lasted for several hundred milliseconds during visual pursuit, although the speed of the stimulus was the same. For instance, smooth eye velocity 400 ms after pursuit onset was higher for BM than for SCR stimuli ($F(1, 7) = 8.59$, $p = 0.022$).

Pursuit initiation is influenced by local biological motion perception

To test whether the differences in proximity to the walker among the scrambled stimuli were reflected in the behavioral responses, we tested the correlation between the psychophysics and behavioral responses. We found a strong correlation between the percentage of correct responses in the psychophysics experiment and the level of smooth eye velocity measured 100 ms after pursuit onset in the first behavioral experiment (Figure 2C, fastest target velocity, Spearman correlation: R = 0.78, $p = 0.01$). This correlation was still present 50 ms later (Spearman correlation: R = 0.68, $p = 0.042$) but disappeared afterwards. In addition, for those trials, the average acceleration during pursuit initiation (see Materials and methods) did correlate with the percentage of correct response (Spearman correlation: R = 0.7, $p = 0.036$), a finding that emphasizes the differential influence of perceptual mechanisms on pursuit initiation and maintenance (Wilmer & Nakayama, 2007).

Saccades cannot account for the differences in behavior

In addition, we investigated whether the saccades might be responsible for the observed difference in smooth eye velocity evoked by the point-light walker or the scrambled stimuli. We found no significant difference in saccade latency, with respect to the stimulus motion onset (BM vs. SCR, ANOVA: $F(1, 7) = 2.66$, $p = 0.15$) or to pursuit onset ($F(1, 7) = 0.27$, $p = 0.87$). On average, saccade latency was 113 ms after pursuit onset. Catch-up saccade accuracy was not influenced by the stimulus type ($F(1, 7) = 0.001$, $p = 0.97$) even though stimulus type tended to influence the amplitude of catch-up saccades ($F(1, 7) = 3.66$, $p = 0.09$). The amplitude of the saccades in response to the scrambled stimuli (mean = 2.03°, $SD = 0.90$) was slightly larger than with the biological motion stimulus (mean = 1.94°, $SD = 0.87$°). As the saccadic amplitudes evoked by the scrambled stimuli tended to be larger than for the BM stimuli, any hypothetical bias of saccades on the measure of smooth pursuit velocity would reduce the observed difference in smooth eye velocity between BM and SCR.

Inversion of the point-light walker influences smooth pursuit

We also performed a third experiment, where the scrambled stimuli were replaced by an inverted point-light walker. In this experiment, we were able to reproduce the results obtained with the scrambled stimuli. We found no difference in pursuit onset in the smooth pursuit response elicited by the point-light walker and inverted point-light walker stimuli (BM vs. INV, $F(1, 9) = 0.17$, $p = 0.69$). In contrast, 200 ms after pursuit onset, the smooth pursuit response elicited by the upright point-light walker was higher than the response elicited by the upside-down walker (Figures 3 and S2, ANOVA: $F(1, 9) = 16.06$, $p = 0.003$). This difference lasted a few hundreds of milliseconds. Indeed, at 400 ms, the smooth eye velocity was different between the two stimuli ($F(1, 9) = 34.5$, $p = 0.0002$). Again, catch-up saccade latency, amplitude or accuracy was not different between the two conditions (ANOVAs, latency: $F(1, 9) = 0.051$, $p = 0.83$; amplitude: $F(1, 9) = 0.019$, $p = 0.89$; accuracy: $F(1, 9) = 0.03$, $p = 0.86$).

Biological motion facilitates smooth pursuit

Finally, to test whether normal biological motion facilitated pursuit or scrambled biological motion impaired pursuit, we analyzed the trials during which only the hip dot was presented on the screen. Indeed, it has been reported that adding coherently moving dots facilitates smooth pursuit eye movements (Heinen & Watamaniuk, 1998; Watamaniuk & Heinen, 1999). Therefore, we compared the smooth pursuit response to the BM, INV and DOT stimuli. Interestingly and consistently with those studies, we found that pursuit velocity was higher for the BM and INV stimuli than for the DOT stimuli during the very early part of the pursuit response. Indeed, at 50 and 100 ms, smooth eye velocity was larger for the BM and INV than for the DOT stimulus (Tukey Post-Hoc test: BM vs. DOT: $p = 0.013$ and INV vs. DOT: $p = 0.003$). In contrast, 200 ms after pursuit onset, when we observed a difference between the smooth eye velocity elicited by the BM and INV stimulus, the response to the DOT stimulus was smaller than to the BM stimulus (Tukey Post-Hoc: $p = 0.03$) but not different from the INV stimulus (Tukey Post-Hoc: $p = 0.4$). This last result shows that biological motion did facilitate smooth pursuit eye movements.

Discussion

In the present study, we reported an effect of the proximity of the stimuli to the walker on the smooth eye velocity during a visual tracking task. In line with the differential effects of perception during pursuit initiation and maintenance (Rasche & Gegenfurtner, 2009; Wilmer & Nakayama, 2007), we found that, during pursuit initiation, smooth eye velocity was modulated by the proximity of the scrambled stimuli to the walker measured during our psychophysics experiment. In addition, during pursuit maintenance, smooth eye velocity was higher for a point-light walker than for a scrambled stimulus or

inverted point-light walker. As in many other studies (Billino, Bremmer, & Gegenfurtner, 2008b; Hiris, 2007; Hunt & Halper, 2008; Ikeda, Blake, & Watanabe, 2005; Lange, Georg, & Lappe, 2006; Pavlova, Lutzenberger, Sokolov, Birbaumer, & Krageloh-Mann, 2007; Saygin, Driver, & de Sa, 2008), we used Cutting's algorithm to simulate the point-light walker stimulus. We considered the use of this algorithm to create our stimuli as a worst-case scenario, since it has been argued that it could be suboptimal, compared with biological motion stimuli from human motion recordings. Therefore, the difference between the biological and non-biological conditions could have been even bigger, if we had used a point-light walker based on data from actual human actions; even though, to our knowledge, the difference between those techniques has never been clearly demonstrated.

Rather than the proximity to the walker, could the differences in smooth pursuit response be due to attentional effects? Indeed, it has been shown that divided attention decreases smooth eye velocity during pursuit (Souto & Kerzel, 2008). We could also interpret the dots of the scrambled walkers as distractors, which would reduce the ability of underlying motion detectors to extract target motion information. If motion processing was impaired by the scrambling of the dots, we would predict that the accuracy of the first catch-up saccades would be deteriorated as catch-up saccade amplitudes are influenced by target motion information (de Brouwer et al., 2002; de Brouwer, Missal, & Lefèvre, 2001; Orban de Xivry, Bennett, Lefèvre, & Barnes, 2006; Orban de Xivry, Missal, & Lefèvre, 2008; Schreiber, Missal, & Lefèvre, 2006). Indeed, Newsome, Wurtz, Dursteler, and Mikami (1985) showed that temporary lesion of the area MT, which is essential for motion perception (Born & Bradley, 2005), impairs both the smooth pursuit performance and the accuracy of catch-up saccades. Similarly, if attention was divided by the scrambled process because subjects had to pay attention to several points, we would predict that the catch-up saccades should be delayed by the divided attention (Souto & Kerzel, 2008). In our data, we did observe neither a difference in catch-up saccades accuracy nor a difference in catch-up saccade latency. In sum, neither attentional factors nor increased noise due to the scrambling process is likely to explain the difference in behavior elicited by the BM and SCR stimuli.

The same reasoning can be applied to interpret the difference in smooth pursuit elicited by BM and INV stimuli. Since the inversion of the walker is less susceptible to increase the level of noise as the shape of the walker is still perceptible after the inversion (Sumi, 1984) and since the accuracy of catch-up saccades was not different between the point-light walker and its upside-down version, we do not believe that an increased level of noise due to the inversion was responsible for the differences in smooth pursuit velocity.

Of course, this does not mean that attention does not play a role in biological motion processing. However, it shows that the attentional load is similar in both conditions as it is required to process biological motion stimuli (Cavanagh, Labianca, & Thornton, 2001; Thornton, Rensink, & Shiffrar, 2002; Thornton & Vuong, 2004) or to filter out irrelevant motion signals (Khurana & Kowler, 1987; Spering & Gegenfurtner, 2007; Spering, Gegenfurtner, & Kerzel, 2006). In addition, the correlation we found between the results from the psychophysics and behavioral experiments suggests that local motion cues, which are not impaired by the scrambling process and which are processed by the bottom-up pathway, influence the smooth pursuit initiation. Their influence was only detectable during the pursuit initiation (first 150 ms of the response). This is reminiscent of the early influence of the low-level motion processing pathway on pursuit initiation (Wilmer & Nakayama, 2007). Importantly, dividing attention has little effect on the low-level, bottom-up pathway (Thornton et al., 2002) and therefore, attentional factors would not account for this observation. Finally, we believe that attentional factors might not account for our results, as the smooth pursuit to the INV stimuli does not appear deteriorated when compared to a single dot stimulus. Therefore, biological motion facilitates smooth pursuit.

The effect of biological motion on oculomotor response might result from the activation of a specific neuronal pathway for biological motion processing (Grossman et al., 2005, 2000; Saygin, 2007; Saygin et al., 2004). Evidence from single neuron recordings suggests that the region of the superior temporal sulcus (STS) of the macaque monkey is specifically involved in the perception of biological motion. The network dedicated to biological motion perception is partially independent of the low-level motion perception network (first- and second-order motion). Indeed, in humans, disruption of the motion-sensitive, middle temporal area (MT) did not affect the perception of biological motion (Billino et al., 2009; Saygin, 2007; Vaina et al., 1990), whereas a lesion in MT reduced low-level motion perception (Komatsu & Wurtz, 1989) and impaired smooth pursuit eye movements in monkeys (Dursteler & Wurtz, 1988; Newsome et al., 1985). Similarly, psychophysics testing of the low-level motion perception network (speed discrimination, coherent motion detection, etc.) showed that processing of motion degraded with age (Gilmore, Wenk, Naylor, & Stuve, 1992; Norman, Ross, Hawkes, & Long, 2003; Sekuler, Hutman, & Owsley, 1980; Warren, Blackwell, & Morris, 1989), whereas the perception of biological motion did not (Billino, Bremmer, & Gegenfurtner, 2008a; Norman, Payton, Long, & Hawkes, 2004). In contrast, the third-order motion processing system, which is strongly influenced by attention (Lu & Sperling, 2001), was necessary for perceiving biological motion (Garcia & Grossman, 2008). For instance, patient studies demonstrated that lesions in the parietal lobe degraded third-order and biological motion perception, while low-level motion perception remained intact (Battelli, Cavanagh, &

Thornton, 2003; Billino et al., 2009). In sum, there are at least two different motion processing pathways: the classical one, which involves area V5/MT (Born & Bradley, 2005) and a second, which might rely on the STS area (Barraclough, Xiao, Oram, & Perrett, 2006; Perrett et al., 1985) and be subservient to biological motion perception. The relative independence of the biological motion and low-level motion perception networks, together with our results, suggests that the biological motion perception pathway might directly influence the smooth pursuit network (Ilg & Thier, 2008).

It might also be possible that the biological motion network changes the activity in areas MT/MST, which in turn affect smooth pursuit. Indeed, the fact that the latency did not differ between the conditions and that pursuit velocity differed significantly only from 150 ms after pursuit onset would be compatible with this hypothesis. This possibility is supported by anatomical studies, which showed the existence of direct and indirect projections from STPa to the MT complex (Boussaoud, Ungerleider, & Desimone, 1990) and studies about implied biological motion, which are in favor of this hypothesis (Jellema & Perrett, 2003; Kourtzi & Kanwisher, 2000; Kourtzi, Krekelberg, & van Wezel, 2008). Therefore, it might be that the enhanced smooth pursuit response to BM resulted from a top-down projection from STPa to the MT complex, which is the main input of the smooth pursuit system. These feedback projections might also explain why people are better at discriminating biological motion than translational motion (Neri, Morrone, & Burr, 1998).

To disambiguate between those two hypotheses (direct input to the smooth pursuit network or feedback projections to the MT complex), one would need to study patients with lesions covering the MT complex but not the STS. In this case, smooth pursuit eye movements would be heavily affected (Dursteler & Wurtz, 1988; Newsome et al., 1985) but biological motion perception would be preserved (Billino et al., 2009; Saygin, 2007; Vaina et al., 1990). For those patients, the direct input hypothesis would predict that their smooth pursuit response would be impaired to a lesser extent for biological motion stimuli. In contrast, the feedback projection hypothesis would predict that the impairment of the smooth pursuit response would be similar for both biological and non-biological stimuli.

Our study highlights the necessity to integrate perception and retinal slip as one input to the smooth pursuit system (Krauzlis & Stone, 1999), independently of the network that subserves motion perception. In this respect, because sensitivity for biological is higher than for translational motion (Neri et al., 1998), we would expect that our smooth eye velocity will also be more sensitive for biological motion than for translational motion.

In our psychophysics experiment, we interpret the percentage of correct responses as the proximity of the stimulus to the walker and the response time as the uncertainty about its direction. We are not aware of any other studies reporting a gradual effect of scrambling on biological motion. Here, we showed that biological motion perception is not an ON–OFF mechanism (as shown during pursuit initiation), but that local motion cues are sufficient to infer a certain degree of biological motion (for example if the movement of the feet is still present, Chang & Troje, 2009). Similar local motions, however, can yield different degrees of biological motion, which could be explained by the importance of particular points from the display (Casile & Giese, 2005; Troje & Westhoff, 2006). However, even if local motion produced a good perception of the heading direction for some stimuli, the shortest response times recorded during our psychophysics experiment were still much longer than response times for biological motion (on average, larger than 1100 ms for SCR and around 750 ms for BM).

In conclusion, we demonstrated that smooth pursuit eye movements are sensitive to the degree of proximity to the walker of the tracked target. These results suggest that the biological motion perception network is an important input to the smooth pursuit system and can modulate transformation of visual signals into eye movement commands. Therefore, biological motion is relevant to both perception and action.

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